THE MORPHOLOGY AND RELATIONSHIPS OF *RACHIOPTERIS CYLINDRICA* WILLIAMSON

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HENRY SMITH HOLDEN

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SYNOPSIS

The anatomy of *Psalixochlaena cylindrica* (Will.), a fern from the Coal Measures, originally described by Williamson as *Rachiopteris cylindrica*, is described and its affinities with other possibly related Palaeozoic ferns is discussed.

The anatomy of *Rhabdoxylon dichotomum* gen. et. sp. nov., also a Palaeozoic fern formerly interpreted as a marsh ecotype of *Rachiopteris cylindrica*, is described and its probable affinities indicated.

INTRODUCTION

THE earliest account of the morphology of the Coal Measure fern which forms the subject of this paper was that of Williamson (1878) who assigned it to his comprehensive genus *Rachiopteris* and created a new species *R. cylindrica* for its reception. His material which appears to have been inadequate for more than a brief description was obtained from a Halifax locality and he regarded its inclusion in the genus *Rachiopteris* as purely provisional. A more detailed account based on the sections in the Cash and other collections in the Manchester University Museum was published by Hick (1896). It is probable that the sections described by Hick were also from the Halifax district since those in the Cash Collection at least were prepared by James Binns who resided in that area. Hick, although inclined to the view that *R. cylindrica* was a fern, left the question of its affinities undecided. In the light of our further knowledge, however, it is now generally agreed that it should be assigned to the Filicales.

A more detailed study of the plant was made by the late Helen Bancroft (1915) who examined not only the specimens described by Hick and by Williamson but also the specimens which the late F. W. Oliver had purchased over a period of years for University College (London). In addition she studied the relevant slides in the Cambridge University Collections and those belonging to the late W. T. Gordon. All the material studied by her came from Yorkshire localities and she suggested that the plant may have been confined to the Yorkshire coalfield. There is no doubt, however, that it occurred elsewhere though less commonly since there are now records of its discovery in coal-balls from Burnley, Bacup and other localities on the Lancashire side of the Pennines. There is also a solitary section (Scott Coll. 2012) from Booth Hill Colliery, near Oldham. It is worthy of note that, apart from its occurrence in coal-balls from both Lancashire and Yorkshire, it has now been recorded and figured by Leclercq (1925) from Belgium and by Kraentzel (1934) from both Holland and Belgium.

Bancroft, on the basis of the specimens examined by her, included two types of stem which she designated as Types α and β in *Rachiopteris cylindrica* her Type α stem having a larger stele and a much more robust build than Type β which she interpreted as representing the semi-aquatic or marsh variety of the species. It should be pointed out, however, that Williamson only applied the name *Rachiopteris cylindrica* to the specimens grouped by Bancroft under her Type α although he referred to and figured a transverse section of a stem clearly belonging to her Type β (Williamson 1878, pl. 24, fig. 88) which he suggested might well be related to *R. cylindrica*.

The present account is based very largely on specimens in the Kidston and Scott Collections together with those in the collection of the author. In addition to these the slides in the Oliver Collection now, like those of the author, in the Department of Palaeontology, British Museum (Natural History), and those in the Williamson Collection have been re-examined as well as individual slides from other sources. The study of this relatively large number of specimens has led to a fuller knowledge of the plant and to a re-assessment of its systematic position and of its relationships to the other Palaeozoic ferns usually included in the Botryopterideae.

It is proposed to describe first the plant named *Rachiopteris cylindrica* by Williamson (i.e. Bancroft's Type α) and to describe and discuss the relationships of Bancroft's Type β later in this paper.

SYSTEMATIC DESCRIPTION

Genus ***PSALIXOCHLAENA*** nov.

Diagnosis. A fern possessing a slender stem with the immature parts at least densely clothed with unbranched multicellular hairs ; stem stele cylindrical consisting entirely of tracheids differentiated into a central group of small tracheids enclosed by a peripheral system of larger ones. Protoxylem mesarch forming two to five groups lying at the junction of the large and small tracheidal members of the stele. Xylem surrounded by a continuous sheath of xylem parenchyma, phloem and phloem parenchyma. Cortex differentiated into parenchymatous inner zone, sclerized middle zone and narrow parenchymatous outer zone ; branching of the stem unequal the daughter stem always smaller then the parent stem and, in most cases, initially possessing two immersed protoxylem groups though occasionally possessing one only. Petioles arising from the stem singly at irregular intervals, circinately coiled when young with a monodesmic vascular supply consisting near its base of a flattened xylem cylinder with the protoxylem at first distributed discontinuously along its adaxial face but soon forming three well-defined ridges : developing a pronounced abaxial curvature distally and thus becoming C-shaped in transverse section. Pinna traces monarch, marginal, given off alternately from the right and left sides of the parent strand and bifurcating repeatedly. Roots uniformly diarch with well-defined endodermis and exodermis. Root hairs present and probably persistent.

Type species. *Psalixochlaena cylindrica* (Will.).

Psalixochlaena cylindrica (Williamson) nov. comb.

Pls. 8, 9; Pl. 10, figs. 1–4

1878 *Rachiopteris cylindrica* Williamson, p. 351, pl. 24, figs. 80–84, 86, 87.
1896 *Rachiopteris cylindrica* Will.: Hick, p. 1, pl. 1, fig. 5.
1908 " *Rachiopteris cylindrica* " Will.: Tansley, p. 14, text-fig. 14.
1908 *Rachiopteris cylindrica* Will.: Scott, p. 333.
1910 *Botryopteris cylindrica* (Will.) Seward, p. 438, text-figs. 305A, B.
1915 *Rachiopteris cylindrica* Will. (Type α): Bancroft, p. 532, pl. 26, figs. 1, 2, 6; pl. 27, figs. 1, 3, 4; text-figs. 1–7, 9, 10.
1920 *Botryopteris cylindrica* (Will.): Scott, p. 345, text-fig. 156.
1923 *Botryopteris cylindrica* (Will.): Bower, p. 121, text-fig. 114.
1925 *Botryopteris cylindrica* (Will.): Leclercq, p. 58, pl. 46, figs. 8, 9; pl. 47, fig. 10.
1926 *Botryopteris cylindrica* (Will.): Bower, p. 10, text-fig. 312.
1927 *Botryopteris cylindrica* (Will.)—Forma α—: Hirmer, p. 533, text-figs. 648, 649.
1940 *Botryopteris cylindrica* (Will.): Walton, p. 100, text-fig. 75.

Diagnosis. As for genus.

Holotype. A transverse section of the stem figured by Williamson (1878, pl. 24, fig. 80). Williamson Colln. slide no. 179.

Description. *Stem*: The stem varies in diameter, in the specimens measured, from 2·0 to 2·3 mm. and that of the stelar xylem from 0·7 to 0·8 mm. The latter consists entirely of tracheids which form a cylindrical core to the stem except where their symmetry is modified by the emission of petiole or root traces or by branching (Pl. 8, fig. 2). In typical specimens the central part of the xylem cylinder is formed of relatively small tracheids surrounded by a zone of tracheids of larger diameter the protoxylem groups, varying in number from two to five, lying at the periphery of the smaller, centrally situated ones and hence being mesarch in position (Pl. 8, fig. 1). Variations from this type of structure are infrequent but very rarely specimens occur in which there is a single centrally situated group of protoxylem, that is, in which the protoxylem is centrarch (Bancroft, 1915, pl. 26, fig. 2).

A still more unusual departure from the typical stelar condition is illustrated by two transverse sections of a stem (Holden Colln. nos. 618, 619) which has been cut transversely at a level at which there are four outgoing root traces and where the stem is preparing to branch. As in typical specimens the xylem of the stem is differentiated into a central group of small tracheids surrounded by tracheids of larger calibre. It differs, however, in possessing an additional cylinder of small tracheids external to the larger ones (Pl. 9, fig. 8). The cells of the conjunctive parenchyma immediately external to these small tracheids have divided in a number of places to form flattened cambiform daughter cells. Whether this indicates that the system of small peripherally situated tracheids is of secondary origin is, however, a matter of some doubt since they show no indication of the regular radial arrangement typical of secondary xylem.

The pits, which are present on all faces of the tracheids, vary from the reticulate type with transversely elongated pits on the wider walls to the scalariform type on those which are narrower. There has been some doubt as to the nature of the

thickening of the tracheids forming the protoxylem. Bancroft considered that this was scalariform and that the type of thickening was possibly to be correlated with relatively slow growth. The thin sections made possible by modern " peel " techniques have shown, however, that these possess spiral thickenings, a feature which they share with the petiolar protoxylem. The xylem is surrounded by a continuous zone of xylem parenchyma, phloem and phloem parenchyma the phloem consisting of a more or less continuous series of large sieve tubes enclosed on either side by the smaller and frequently somewhat tangentially flattened cells of the xylem and phloem parenchyma respectively. External to the phloem and its associated parenchyma there is usually a fairly well defined layer of cells with dark contents which may be interpreted as an endodermis (Pl. 8, fig. 2, Pl. 9, fig. 2). The cortex is divisible into three zones the innermost of which is parenchymatous. The middle cortex is composed of thick-walled cells and, together with the stelar xylem, is, in the less well preserved examples, the only tissue surviving petrifaction. Even when the stele and all the tissues up to and including the middle cortex are present it is very rare to find any trace of the outer cortex and surface tissues. The erosion of these tissues renders it difficult to determine what their normal character was during life though Bancroft has recorded and figured their local survival (Bancroft, 1915, text-fig. 4*a–c*). From her figures it seems probable that the epidermis bore multicellular hairs and this view is strengthened by the good fortune of the author in possessing an obliquely longitudinal section (Holden Colln. 611) passing through the apex of the stem and a series of transverse " peels " (301D 60–70) also passing through the apical region. Text-fig. 1 illustrates the general build of the obliquely longitudinal section which shows, at the lower end, an oblique section of the stem stele from which both a root and petiole trace are being given off. Some distance nearer the apex a root cut transversely is shown embedded in the tissues of the cortex. The apex itself clearly has the form of a blunt dome-shaped mass to the right of which is a very young petiole still showing a circinately coiled apex. Both stem apex and young petiole are surrounded by a dense sheath of unbranched multicellular hairs. The dotted line in Text-fig. 1 indicates the extent of the hair sheath and this and the apex of the stem are also illustrated in Pl. 8, fig. 3. The transverse sections one of which is shown in Pl. 8, fig. 4, demonstrate the same feature and show that the apical tissues of the stem consist of small-celled parenchyma. It has not, however, been possible to demonstrate the existence or otherwise of a single apical cell. A section taken at a somewhat lower level where the tracheidal system is still not fully differentiated also shows that the surface hairs are present and abundant at that level (Pl. 8, fig. 5).

The branching of the stem is always unequal the stele of the daughter stem being smaller than that of the parent. In preparation for branch formation the stele becomes ovoid in section and the protoxylem group destined to supply the branch usually divides into two these passing into that part of the stele which is to form the vascular supply of the branch (Pl. 8, fig. 2). At a higher level the stele of the branch becomes separated from that of the parent stem by the inward extension of the cortical tissues the daughter stele having an oval outline as seen in transverse section with the two protoxylem groups lying one on each side of the mid-line

and situated somewhat nearer the adaxial than the abaxial side (Pl. 8, fig. 1). This stage is well shown in Williamson Colln. slide 187 and is figured by Seward (1910, text-fig. 305B) and by Scott (1920, text-fig. 156A). Exceptionally the protoxylem group supplying the branch does not divide into two and occupies a median position in the branch stele. An example of this kind is figured diagrammatically

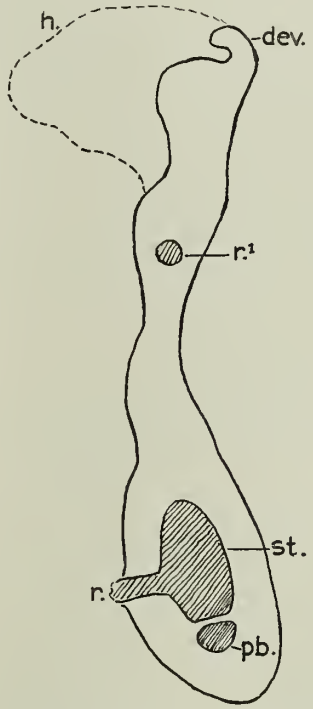


FIG. 1. *Psalixochlæna cylindrica* (Will.) Camera lucida outline of an obliquely longitudinal section passing through the stem apex. *st*, stem stele giving off petiole bundle, *pb*, and root, *r* : r^1, root cut transversely passing through the stem cortex : *dev*, developing petiole showing circinate vernation: *h*, dotted outline indicating extent of the hair sheath. × 12. (Holden Coll., no. 611).

by Bancroft (1915, text-fig. 1). There is some variation in the diameter of the tracheids forming the metaxylem of the branch. As a general rule these tracheids have the same dimensions as those of the parent stem but there are a number of examples (e.g. Holden Colln. 301*a*) in which they are appreciably smaller in diameter and the differentiation into small central and larger peripheral tracheids is not evident.

Petiole : The initial stages in the emission of the petiole trace bear a strong resemblance to those leading to the giving off of a branch. The assumption of the ovoid appearance of the stem stele in transverse section and the positioning of one

of the stem protoxylem groups in the outgrowing metaxylem are, as far as one can judge, identical.

Whilst, however, the branch stele departs as a concentric structure with the protoxylem groups surrounded by metaxylem the departure of the petiole trace is heralded by the development of a strip of parenchyma on the inner side of the petiolar protoxylem. This parenchyma gradually extends to the margin of the stem stele thus separating off the petiole trace as a flattened cylinder with the protoxylem on its adaxial face. The behaviour of the protoxylem varies to some extent but it appears, in most specimens, to consist of a flattish strip of small tracheids extending discontinuously along the greater part of the adaxial face of the petiole trace. As the trace moves further out from the stem stele the protoxylem becomes divided into three definite groups though the ridges so formed do not project from the adaxial face of the metaxylem as prominently as they do in *Botryopteris ramosa* and other Coal Measure species of *Botryopteris*. Another feature which is frequently demonstrable at this stage is the greater diameter of the tracheids of the petiole trace compared with those of the parent stem. This difference in diameter which is characteristic of *Botryopteris antiqua*, *B. hirsuta* and *B. ramosa* does not, however, always occur in *Psalixochlaena cylindrica*. It is well shown in Pl. 9, figs. 1, 2, 9. In many specimens the petiole trace shows no further modification at the level of its separation from the parent axis though Bancroft (1915) mentions the fact that "there is occasionally a slight indentation on the abaxial margin of the strand". This abaxial "indentation" is, in fact, the initial stage in the abaxial curvature of the petiole trace. It is clearly shown in Pl. 9, fig. 2 and becomes steadily more pronounced the further the petiole becomes separated from the parent stem so that, when fully established the stele has a crescentic outline as seen in transverse section with the protoxylem on the convex, adaxial side and has the shape of an inverted gutter. This abaxially curved petiole trace is clearly different from that typical of the various species of *Botryopteris* and much more nearly resembles that of *Tubicaulis*. The progressively greater extent of abaxial curvature is illustrated in Pl. 9, figs. 3, 6, 7 and culminates in the condition shown in Pl. 9, fig. 7. All the isolated petioles in the Scott Collection which are now identified with *Psalixochlaena cylindrica* were grouped by Scott in the genus *Selenochlaena*. He included his specimens under that head simply as a matter of convenience until their relationships could be established. *Selenochlaena* was a genus originally established by Corda (1845) in his revision of the fossil plants studied by Cotta (1832). Cotta's genus *Tubicaulis*, in the wide sense originally used by him, included representatives of Palaeozoic ferns which have since been transferred to other genera (e.g. *Ankyropteris* and *Etapteris*) and *Tubicaulis solenites* is the only one of those he described now recognized as a valid species. Corda's transfer of *T. solenites* to *Selenochlaena*, as Stenzel (1889) pointed out in his survey of the genus *Tubicaulis*, is invalid and he has correctly restored it to that genus.

The branching of the petiole, like its vascular supply, is characteristic and unusual. Lateral traces are given off alternately from the right and left sides of the main petiolar strand their emission commencing quite near the base of the petiole and, in some examples, beginning even before this is separated from the stem. In prepara-

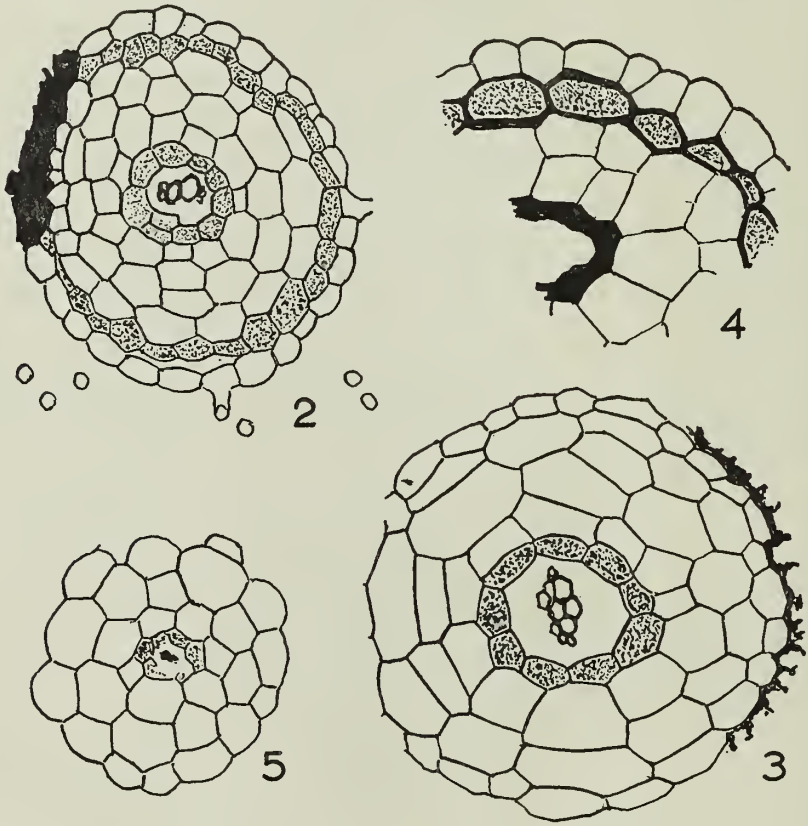
tion for the emission of a branch trace a lateral protoxylem group and its associated metaxylem become detached from the margin of the main trace and, surrounded by phloem and cortical tissues, is separated from the petiole as an initially monarch secondary axis (Pl. 10, fig. 2). One such axis is figured by Bancroft (1915, text-fig. 15) who had not, however, any means of linking it positively with *Rachiopteris cylindrica*. This type of emission of the branch trace is clearly marginal in the sense proposed by Chrysler (1910) and adopted by Davie (1914) and, later by Bower (1923). Once the branch has separated from the petiole it appears invariably to dichotomize and, in some examples at least, to dichotomize repeatedly. Pl. 9, fig. 4 shows a petiole which has given off a branch to the right the vascular bundle of which is already dichotomizing whilst that destined for a branch from the left hand side of the petiole is still tenuously linked with the main petiolar strand. Pl. 10, fig. 1 shows the major part of a branch in which the vascular bundle has not only bifurcated but in which the daughter steles are again forking equally in their turn. The available evidence suggests that as the lateral protoxylems pass alternately from the petiolar stele they are renewed by the division of the central protoxylem group (Pl. 9, fig. 7).

There is no evidence of the existence of flattened assimilatory pinnae or pinnules such as those recorded in *Botryopteris americana* (Delevoryas & Morgan, 1954*b*) and in *B. forensis* (Renault, 1896) nor is there any satisfactory evidence of the type of sporangium which the plant possessed.

Root system : The roots of the first order usually arise singly from the stem although occasionally two, and exceptionally three or four, may be given off at the same level (e.g. Holden Coll. 618). Their development does not appear to bear any close relation either to the branching of the stem or to the emission of the petioles. They are always diarch with the xylem of the root stele approaching the *Osmunda* type rather than that characterizing the majority of existing leptosporangiate ferns (Pl. 10, fig. 3). As in the stem the pitting of the larger tracheids is reticulate with transversely elongated pits whilst that in the smaller ones adjoinging the protoxylem is scalariform. The thickenings of the minute protoxylem elements are spiral.

Where the xylem of root and stem unite the stem xylem is characterized by the development of a peripheral flat or slightly convex disc of small, tangentially flattened tracheids with which the expanded base of the root-xylem unites (Pl. 8, fig. 2). The roots possess a separate cortex from their point of origin the cells of which, during their passage through the stem tissues, are uniformly somewhat thick-walled and, in the majority of the specimens studied, have dense brown contents. On the emergence of the roots from the stem the thick-walled cortical cells are replaced by parenchyma although they may persist peripherally for a short time. Where the whole of the tissues of the root are preserved the superficial cells are thin-walled and develop root hairs, a feature first recorded by Bancroft. These root hairs are long and locally numerous and appear to be persistent since they are present in what are clearly mature roots (Pl. 10, fig. 4 ; Text-fig. 2). Immediately below the piliferous layer is a well-defined exodermis the cells of which have thickened walls and often possess dark contents. The stelar tissues are enclosed by a readily distinguishable endodermis (Pl. 10, fig. 3 ; Text-figs. 2–5) the cells of which, like those

of the exodermis, usually have dark contents. The state of preservation of the roots, like that of the stems and petioles, is very variable. It is only rarely that the piliferous layer is present and frequently the exodermis is also represented by nothing more than a ragged fringe of broken down cell remains (Text-fig. 3). The branching of the roots is monopodial. The daughter roots and their branches are



FIGS. 2–5. *Psalixochlœna cylindrica* (Will). Camera lucida drawings of transverse sections of roots.

FIG. 2. T. S. of small root in which all the tissues except the phloem are preserved : note the presence of root hairs. × 90. (Holden Coll., no. 615).

FIG. 3. A similar section in which the piliferous layer is missing and in which the exodermis, here shown in part only, is represented by a ragged fringe of cell remains. × 150. (Holden Coll., no. 301, C1).

FIG. 4. Part of a somewhat oblique section of a very small root showing the endodermis, cortex, exodermis and piliferous layer. × 200. (Scott Coll., no. 1535).

FIG. 5. T.S. of a minute root in which the piliferous layer and the exodermis have been lost. × 130. (Holden Coll., no. 301, C1).

All the figures show the large, very regular cortical cells which are characteristic of these roots.

characterized by large and very regular cortical cells which form a most distinctive feature (Text-figs. 2–5). These daughter roots were figured by Williamson (1878, pl. 24, figs. 81–85). Figures 81, 82 and 83 are described as " Transverse sections of three successively smaller stems " whilst his fig. 85 shows part of the root in fig. 83 more highly magnified. In fig. 85 the large cortical cells and the dark cells of the endodermis are clearly shown and it may be noted that both the exodermis and piliferous layer are missing. Pl. 10, fig. 4 illustrates part of a somewhat thick section showing two rootlets in which not only the endodermis and the exodermis are preserved but also the piliferous layer with numerous long root hairs. The proof that small roots such as these were part of the root system of *Psalixochlaena cylindrica* was only rendered possible by the preparation of a close series of " peels " which enabled the connection between the roots of various sizes to be established. It should be pointed out, however, that a far better picture of the root hair system is provided by the thicker hand ground specimens such as the one described above.

Discussion. Before considering the light thrown on the systematic position of *Rachiopteris cylindrica* Will. by the present investigation it will be helpful to record the views of the various palaeobotanists by whom it has been mentioned. Tansley (1908) retained Williamson's name though he placed this in inverted commas. Scott (1908) also used Williamson's name but pointed out (p. 333) that whilst it had been proposed to include it in the genus *Botryopteris* its habit differed so markedly from that of other Botryopterideae that it would perhaps be preferable to establish a new genus for it. Seward (1910 : 438–440) whilst quoting Scott's opinion was the first to include the species in *Botryopteris*. It is interesting to note that, although Bancroft's paper (Bancroft, 1915) was not published until five years later, she reverted to Williamson's name though she observed that other authors had considered that the plant should be included in the genus *Botryopteris*. One of the reasons for Bancroft's retention of the name *Rachiopteris cylindrica* appears to be that her study was undertaken in the Botany Department of University College (London) which at that time was directed by the late Professor F. W. Oliver. The card index of the Oliver Collection of fossil plants has two entries dealing with the plant in question though it has not been found possible to discover which of them was first made. One of them reads " *Rachiopteris cylindrica* (generally included in *Botryopteris* but probably a different genus) " whilst the other reads " *Rachiopteris cylindrica* (inc. in Botryopt. but really diff. genus) ". It seems clear from these entries that Oliver had considerable doubts about the validity of transferring Williamson's plant to the genus *Botryopteris* and that this doubt influenced Bancroft in retaining the non-committal generic name used by Williamson.

Scott (1920 : 345–349) subsequently followed Seward's example and referred the plant to *Botryopteris* as *B. cylindrica* though obviously with some reservations. Bower (1923 : 121 ; 1926 : 10–11) and Leclercq (1925) also accepted its inclusion in *Botryopteris* as did Hirmer (1927 : 532–534) who includes it as one of the typical species of the genus. Still more recently Walton (1940 : 88–101) has also included it in his Botryopterideae among the remaining species of *Botryopteris*.

Recent discoveries in Great Britain and the United States of America strongly suggest, however, that the time is ripe for a critical re-survey of the genus *Botryopteris*

and the species which at present are assigned to it. Of the British species *Botryopteris antiqua* from the Lower Carboniferous of Scotland has recently been the subject of detailed study by Surange (1952) who has added considerably to our previous knowledge of this plant though further investigation is desirable when suitable material is available. The same author (Surange, 1954) has also described under the name *Botryopteris elliptica* a rachis from the Coal Measures bearing a bud on its abaxial face. The specimen bears a close resemblance to similar buds described by Long (1943) who assigned his specimens to *B. hirsuta*. Neither Surange nor Long, however, were able to demonstrate any connection between their bud-bearing rachises and the main stems from which they had, presumably, arisen.

The comparatively brief descriptions of *Botryopteris hirsuta* and *B. ramosa* given in Scott (1908, 1920) and similarly short references in Seward (1910), Hirmer (1927) and Walton (1940) are apparently the only published sources of information on these species apart from those in Williamson's early records. Scott himself (1920 : 339) has suggested the possibility that specimens of other species had been assigned to one or other of the two named ones and it is evident that a detailed study of both species and other possibly related plants is highly desirable.

The investigation of the fossil plants from American coal balls has yielded much information about specimens of *Botryopteris* occurring in the United States. Some of these show a considerable resemblance to *B. forensis* from the French Permo-carboniferous notably that described by Darrah (1941) and later and more fully described by Delevoryas & Morgan (1954*b*). These authors correct Darrah's account (Darrah, 1941) of the method of departure of the lateral trace from the petiole strand and establish this as marginal. *B. americana*, the species described, shares with the French species, *B. forensis*, the petiole trace with its "omega-shaped" cross section and the possession of flattened pinnules as well as the stout unbranched hairs with their characteristic septa. Nothing is yet known of the stem of this species but Delevoryas & Morgan (1954*b*) suggest that the petioles and pinnules they describe may possibly represent the more distal parts of the petiolar system of the species described by Mamay & Andrews (1950) as *B. trisecta*. This species, the petiolar vascular strand of which is very similar to that of *B. americana*, possesses a stem stele which is protostelic with exarch protoxylem, a feature in which it resembles *B. forensis*. In *B. trisecta* the method of division of the primary petiole trace is very distinctive. It branches into three to form a median petiole trace which is omega-shaped in transverse section and two lateral primary pinna traces.

Whether the British and Belgian species and those of American and French origin should be included in the same genus is perhaps becoming a matter of some doubt which may only be resolved by further research as suitable specimens become available. *Psalixochlaena cylindrica* obviously shows a number of features of structural agreement with both the British Coal Measure species *Botryopteris ramosa* and *B. hirsuta* and with *B. mucilaginosa* from the Belgian Coal Measures. It shares with them a stem in which the stele has a protostelic xylem system without parenchymatous inclusions and with mesarch protoxylem, a monodesmic petiole trace with marginally produced branch traces and a superficial covering of unbranched multicellular hairs. The petiole trace is also like that of the *Botryopteris* species in

possessing near its point of origin three adaxially situated protoxylem groups forming well-defined ridges on the side of the trace nearest the parent stem. *Psalixochlaena cylindrica* differs from the *Botryopteris* species in showing some differentiation of the stem stele into a median region of small tracheids surrounded by a peripheral zone of tracheids of larger calibre and in the development in the petiole trace of an abaxial curvature which gives it the form of an inverted gutter this producing a C-shaped transverse section. The abaxial curvature of the petiole trace obviously separates *P. cylindrica* from the various species of *Botryopteris* and suggests comparison with those Palaeozoic ferns which possess a similar type of trace. These are included in the three genera *Tubicaulis*, *Anachoropteris* and *Apotropteris*. Of the three genera *Tubicaulis* has been the most widely studied and includes five species namely *T. solenites* from the Permian of Saxony (Stenzel, 1889), *T. sutcliffii* from the Lower Coal Measures of Lancashire (Stopes, 1906), *T. berthieri* from the Permo-carboniferous of Autun (Bertrand, 1911) and two recently described American species, *T. multiscalariformis* from the Middle Pennsylvanian of Kansas (Delevoryas & Morgan, 1952) and *T. scandens* from the Upper Pennsylvanian of Illinois (Mamay, 1952). All these species agree in possessing a stem stele composed entirely of tracheids with exarch protoxylem and, as far as is known, a petiole trace initiated as a flat or slightly abaxially recurved bar, this developing a more pronounced abaxial curvature in its more distal parts. The protoxylem of the petiole trace appears to be distributed discontinuously along its convex, adaxial face. The place of origin of the pinna traces is not known in *T. sutcliffii* and *T. berthieri* but in the remaining three species they are extra-marginal that is, they arise from the adaxial face of the petiolar strand.

Our knowledge of the genus *Anachoropteris* is less complete, the known species, apart from *A. clavata*, being represented only by their petioles. The petiole strands of both *A. pulchra* and *A. involuta* have strongly inrolled margins whilst those of *A. clavata* (Delevoryas & Morgan, 1954) are more U-shaped in transverse section with two robust groups of comparatively large tracheids forming the arms of the U these being linked by a strip of tracheids of smaller calibre. The only stem recorded for this species is one arising from a large petiole and corresponds in type with that described by Long (1943) in *Botryopteris hirsuta*. The xylem in this stem is wholly tracheidal and the small xylem elements which occur on the periphery of the stele are interpreted as probably the protoxylem . The stele is thus exarch. In all the three species of *Anachoropteris* referred to the pinna traces are extra-marginal in origin.

It is evident that both *Tubicaulis* and *Anachoropteris* differ from *Psalixochlaena cylindrica* in the exarchy of the stem protoxylem and, where this is known, in the extra-marginal mode of departure of the pinna traces.

Apotropteris, with the single known species *A. minuta*, is a Coenopterid fern which has recently been described by Morgan & Delevoryas (1954*a*) from the Upper Pennsylvanian of Illinois. The stem stele shows a certain similarity to that of the Coal Measure plant described by Bancroft (1915) as *Rachiopteris cylindrica*, Type *β*. As in the latter the xylem of the stem stele is wholly tracheidal with a centrarch group of small tracheids with scalariform thickening although, in addition, other similar small tracheids occur grouped round the periphery of the stele. Morgan &

Delevoryas suggest that both the central and peripheral groups of small tracheids may be regarded as protoxylem though only the central group appears to be connected with that of the petiolar vascular supply. The latter is almost as large as that of the stem from which it arises and its emission leaves a large somewhat V-shaped depression on the side adjacent to its departure. At a slightly higher level the petiole trace becomes C-shaped as seen in transverse section with protoxylem on its convex adaxial face and with the concavity abaxial. The mode of departure of the pinna traces is not known.

It will be clear from the description of *Psalixochlaena cylindrica* Will. given in this paper and from what has been stated above that it differs in a number of features both from the various species of *Botryopteris* with which it has been previously linked and from the three genera which it resembles in possessing an abaxially curved petiole trace. A new genus, *Psalixochlaena* (from the arched vascular bundle of the petiole), is therefore instituted for its reception.

Genus ***RHABDOXYLON*** nov.

Diagnosis. A small fern with the stem densely clothed with unbranched multicellular hairs. Stelar xylem wholly tracheidal with a single centrarch protoxylem group. Cortex entirely parenchymatous consisting of an inner zone with abundant intercellular spaces and an outer zone in which these are absent. Stem branching dichotomously and equally. Petiole trace oval in transverse section with a single protoxylem group.

Type species. *Rhabdoxylon dichotomum* n. sp.

Rhabdoxylon dichotomum n. sp.

(Pl. 10, figs. 5–7)

1878 *Rachiopteris cylindrica* Williamson, p. 351, pl. 24, fig. 88
1896 *Rachiopteris cylindrica* Will.: Hick, p. 1, pl. 1, figs. 1–4, 6.
1915 *Rachiopteris cylindrica* Will. (Type β) : Bancroft, p. 532, pl. 26, figs. 3, 4, 7–9 ; pl. 27, fig. 2 ; text-fig. 8.
1920 *Botryopteris cylindrica* (Will.) (β form) : Scott, p. 347, text-fig. 157.
1925 *Botryopteris cylindrica* (Will.) (β form) : Leclercq, p. 58, pl. 47, fig. 11 ; pl. 48, fig. 12.
1927 *Botryopteris cylindrica* (Will.) (Forma β) : Hirmer, p. 533.

Holotype. A stem section (Williamson Colln. 179) figured Williamson (1878 ; 351, pl. 24, fig. 88).

Diagnosis. As for genus.

Description. The plant which Bancroft named *Rachiopteris cylindrica* Will.—Type β and which she interpreted as the marsh or sub-aquatic ecotype of the more robust Type α differs from the latter in a number of features. The stem diameter in the specimens measured ranges from 1·8 to 2·1 mm. and that of the stele from 0·35 to 0·5 mm. The xylem of the stem stele consists entirely of tracheids without any admixture of parenchyma. There is not, however, any differentiation of this into an inner zone of small tracheids and an outer zone of larger elements with the

protoxylem lying at the junction between the two. The single protoxylem group occupies the centre of the xylem mass and may therefore be described as centrarch in position. The xylem is surrounded by a continuous sheath of xylem parenchyma, phloem and phloem parenchyma and the whole of the stelar tissues are enclosed in a relatively wide cortex (Pl. 10, figs. 5, 6). The tissues forming the cortex are divisible into inner and outer zones both of which are composed entirely of parenchyma. The cells of the inner zone are smaller than those of the outer one and show abundant intercellular spaces whilst those of the outer zone are more compact and are devoid of intercellular spaces (Pl. 10, fig. 5). The inner cortex frequently shows partial or complete collapse (Pl. 10, figs. 5, 6) and this may, as in one of the sections figured by Bancroft (1915, pl. 26, fig. 4) lead to the formation of large intercellular cavities separated by radial plates of collapsed parenchyma. A somewhat similar condition is figured by Leclercq (1925, pl. 47, fig. 11) in a section of the plant from Belgium though in this specimen the cavities are less regular than in the one figured by Bancroft. This type of collapse is, however, unusual and in the great majority of cases breakdown results in the formation of a dark irregular strip in which the cellular structure is difficult or impossible to distinguish. The development of large cortical cavities separated by radiating plates of tissue is not uncommon in the petrified material of plants in which the cortical tissues are divisible into a delicate parenchymatous inner part and a more resistant outer part (e.g. *Ankyropteris corrugata*, *A. westphaliensis*). In *A. corrugata* the partial breakdown of the inner cortex to form radiating plates of tissue alternating with wide cavities may take place in the plant whilst the tissues are still healthy and, where this occurs, the cells forming the radial plates of parenchyma proliferate and may partly or wholly fill the cavities (Holden, 1930, pl. 9, fig. 30 ; pl. 10, fig. 32). In other specimens of *A. corrugata* the collapse of the cortical tissues leads to no new growth and it may well be that their collapse occurred when the plant was in a moribund condition. The occurrence of similar radiating plates of parenchyma alternating with wide cavities in the inner cortex of petioles of *A. westphaliensis* was first recorded and figured by Williamson (1874, pl. 58, fig. 49) and more recently by Bertrand (1909 : 76, pl. 10, fig. 72). In none of the specimens examined by the author nor in the specimens referred to above are there any indications of cell proliferation from the radiating plates. The superficial tissues are seldom preserved but when present they develop abundant unbranched multicellular hairs. Excellent examples of these hairs or their bases are shown in Williamson Colln. slide 180, and in slides 631 and 1459 and others in the Kidston Collection. Some of these are shown in Pl. 10, fig. 7 and Text-fig. 6*a–e*. The parenchyma lying immediately below the epidermis is composed of cells which often have bright orange contents and this suggests that they may have been secretory in character.

The branching of the stem, in contrast to that of *Rachiopteris cylindrica* always leads to the formation of two equal daughter axes. The process of division is extremely simple. The centrarch protoxylem group divides into two daughter groups and these become more widely separated by the development of metaxylem tracheids between them the stele assuming an oval outline as seen in transverse section (cf. Bancroft, 1915, pl. 26, fig. 9). This stage is followed by one in which two

equal centrarch daughter steles are formed (Pl. 10, fig. 6) one stele passing to each of the branches.

Petiolar formation is equally simple the stem protoxylem dividing into two and one of these passing into the vascular strand destined for the petiole. This petiolar vascular strand is ovoid in transverse section and possesses a single exarch protoxylem group on its adaxial face (Pl. 10, figs. 5–7). Usually it is much smaller than that of the stem from which it arises (Pl. 10, fig. 6 ; cf. Bancroft, 1915, pl. 26, figs. 3, 7, 8) though occasionally a somewhat larger example is encountered. No examples have been discovered either of the branching of the petiole or of sections showing its more

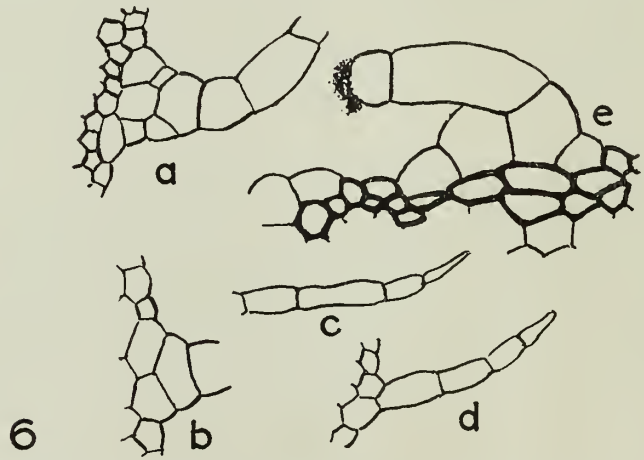


FIG. 6. *Rhabdoxylon dichotomum* n. gen. et sp. Parts of surface hairs. *a*, *b*, basal parts ; *c*, tip of hair from stem ; *d*, complete hair from petiole. All × 80. (Kidston Coll., no. 631) : *e*, base of similar hair from stem, × 100. (Williamson Coll., no. 180).

distal portions so that nothing is known of these characters. The base of the petiole bears numerous unbranched multicellular hairs like those present on the stem (Pl. 10, fig. 7 ; Text-fig. 6*d*).

Although Bancroft (1915) came to the conclusion that the differences between this plant and *Rachiopteris cylindrica* Will. Type α were " caused by the influence of water upon individuals " she did indicate that, among other possibilities, it might be a distinct species. The plant shares with *R. cylindrica* and with the various species at present included in the genus *Botryopteris* a stem in which the xylem consists entirely of tracheids and in which the surface is clothed with unbranched multicellular hairs. It also agrees with them in possessing a monodesmic petiole trace with adaxial protoxylem. It differs in the position of its protoxylem from both *B. forensis* and *B. trisecta* in which this is exarch, and agrees with *Apotropteris* in possessing a centrarch protoxylem though this genus, according to Delevoryas & Morgan, has small peripheral tracheids which may also be interpreted as protoxylem. The fact that no transitions have been discovered which would link *Psalixo-*

chlaena cylindrica with Bancroft's Type β apart from the rare specimens of the former in which the protoxylem of the stem is centrarch suggests that there is a good reason for placing it in a separate genus. It differs constantly in the bifurcation of the stem to form equal daughter axes, in the fact that the petiole trace has a single protoxylem group and in possessing a cortex consisting entirely of parenchyma. It is therefore proposed that an appropriate generic name for this fern is *Rhabdoxylon* (from the rod-shaped xylem of the stem) and it has been given the specific name *Rhabdoxylon dichotomum*.

SUMMARY

Psalixochlaena cylindrica (Will.) is a small fern from the Coal Measures originally assigned by Williamson (1878) to his comprehensive genus *Rachiopteris* as *R. cylindrica* and later transferred by Seward to the genus *Botryopteris* as *B. cylindrica* (Will.). It possesses a stem which branches unequally. The stem xylem consists entirely of tracheids which are differentiated into a central group of tracheids of small calibre surrounded by larger elements. The protoxylem groups, two to five in number, are situated at the junction of the large and small tracheids and are therefore mesarch in position. The cortex is divisible into three zones the inner and outer ones consisting of parenchyma whilst the middle zone is sclerized. The young parts of the stem are densely covered with unbranched multicellular hairs. The petioles, which arise singly, have a vascular supply which is monodesmic and is initially ovoid in transverse section with three adaxial protoxylem groups. In its more distal parts the petiolar vascular supply develops a pronounced abaxial curvature. Pinna traces are given off marginally and alternately from the right and left sides of the petiole trace. They are monarch and branch dichotomously. The roots are diarch with a well-defined endodermis and exodermis and with a cortex composed of very regular cells. The roots bore long root hairs which were probably persistent.

Rhabdoxylon dichotomum gen. et sp. nov. is also a small Coal Measure fern recorded from the same localities as *Psalixochlaena cylindrica*. The stem is covered with a close investment of unbranched multicellular hairs. Its stelar xylem is wholly tracheidal and possesses a single centrarch protoxylem group. The stem cortex is parenchymatous, wide in diameter and is differentiated into an inner zone of small cells with abundant intercellular spaces and an outer zone of larger cells in which there are no intercellular spaces. The stem divides into equal branches. The petioles have a vascular supply which is monodesmic and possesses a single adaxial protoxylem group. The mode of emission of the pinna traces is unknown.

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PLATE 8

Psalixochlaena cylindrica (Will.)

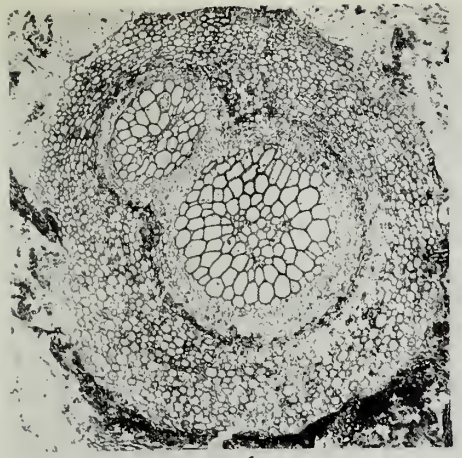
FIG. 1. T.S. of a typical section of a main stem and a branch stele with two protoxylem groups, × 25. (Holden Coll., no. 301, G76).

FIG. 2. T.S. of a stem showing an earlier stage in the emission of a branch and, to the right, the attachment of a root stele, × 35. (Holden Coll., no. 301, D2).

FIG. 3. Longitudinal section through the stem apex showing the close investment of hairs and a circinately coiled young petiole, × 60. (Holden Coll., no. 611).

FIG. 4. T.S. of the stem apex showing the investment of hairs, × 36. (Holden Coll., no. 301, D65).

FIG. 5. Part of a T.S. of a stem near the apex showing the incompletely differentiated stelar xylem and cortex and the surrounding hairs, × 20. (Holden Coll., no. 301, B94).



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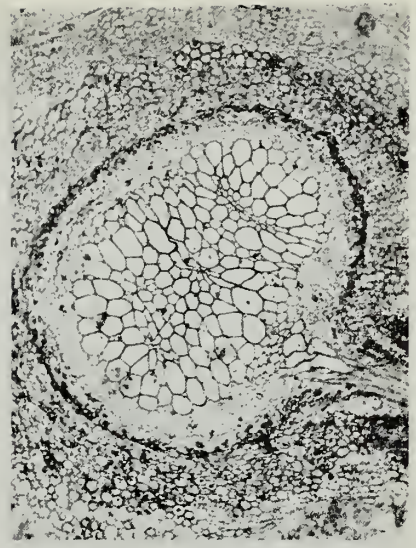

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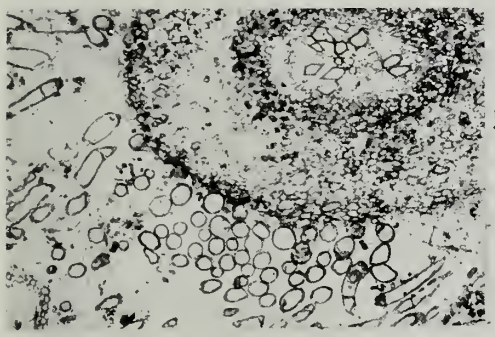

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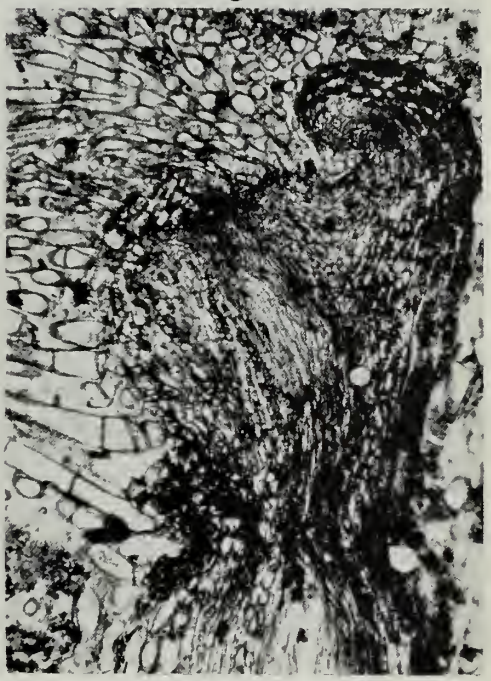

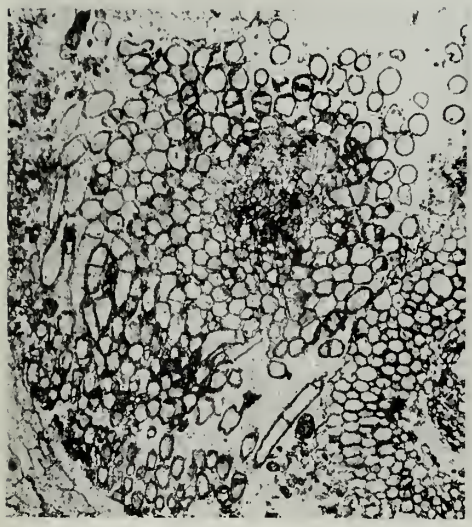

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PLATE 9

Psalixochlaena cylindrica (Will.)

FIG. 1. T.S. of a stem showing an early stage of the emission of a petiole trace, × 40. (Kidston Coll., no. 2027).

FIG. 2. T.S. section of a stem with a petiole trace to the left and a root trace to the right. Note the beginning of the abaxial curvature of the petiole trace, × 25. (Glasgow University Figd. Slide Coll., no. 595).

FIG. 3. T.S. of the vascular bundle of a petiole in which there is only a flattening of the abaxial face. The three adaxial protoxylem groups are clearly shown, × 40. (Kidston Coll., no. 2052).

FIG. 4. T.S. of petiole and pinna. The abaxial curvature of the petiole trace is more evident : the pinna trace to the left is still tenuously attached to that of the petiole : the pinna trace of the separate pinna to the right is already dichotomising, × 25. (Kidston Coll., no. 2050).

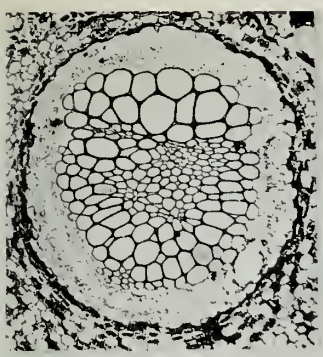
FIG. 5. T.S. of the petiole and attached pinna trace from Fig. 4 more highly magnified, × 40.

FIG. 6. T.S. of a petiolar vascular bundle showing the three adaxial protoxylem groups and a more pronounced abaxial curvature, × 60. (Holden Coll., no. 301, G76).

FIG. 7. T.S. of a petiolar bundle showing the ultimate stage of the abaxial curvature. Note that the central protoxylem group has divided, × 40. (Kidston Coll., no. 1625).

FIG. 8. T.S. of a stem showing an exceptional peripheral zone of small tracheids, × 40. (Holden Coll., no. 618).

FIG. 9. T.S. of a branch giving off a petiole trace. Note the disparity in tracheid diameter between the branch stele and that of the petiole, and the oval outline of the latter, × 25. (Holden Coll., no. 301*a*).



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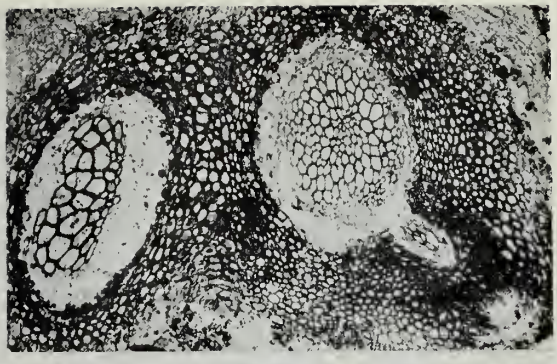

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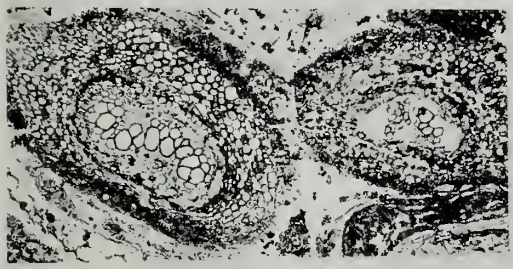

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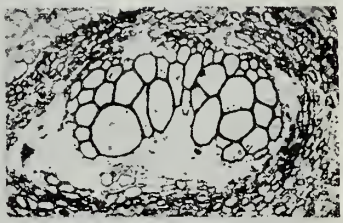

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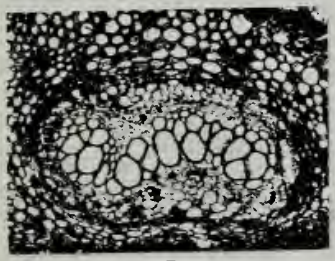

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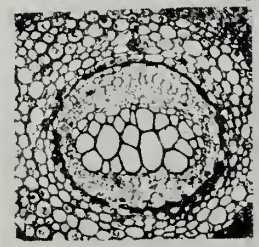

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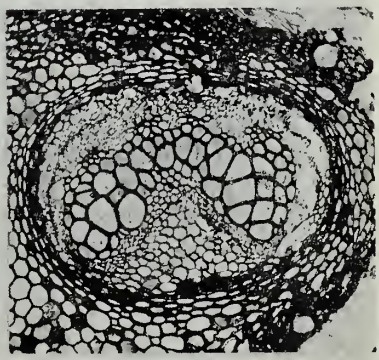

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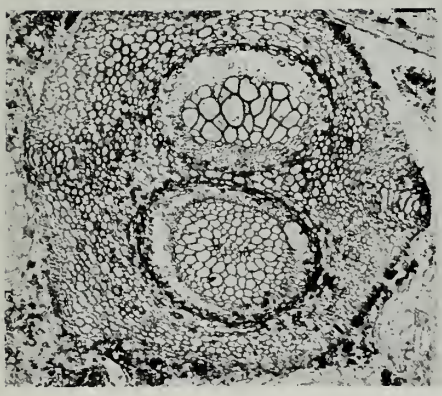

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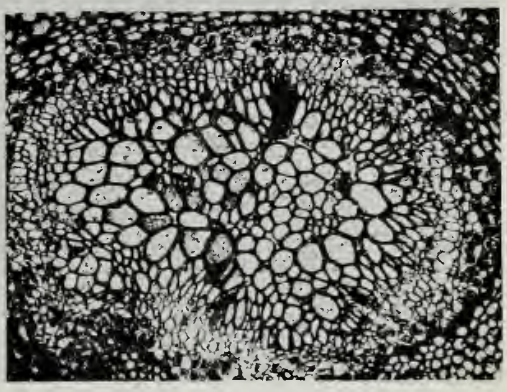


PLATE 10

Psalixochlaena cylindrica (Will.)

FIG. 1. T.S. of a pinna trace in which the vascular bundle has dichotomised and in which the two daughter bundles are also dichotomising, × 50. (Williamson Coll., no. 178).

FIG. 2. T.S. of a monarch pinna trace, × 35. (Oliver Coll., no. K21r).

FIG. 3. T.S. of the vascular bundle of a root of the first order showing the diarch xylem and the phloem and endodermis, × 40. (Holden Coll., no. 301, B13).

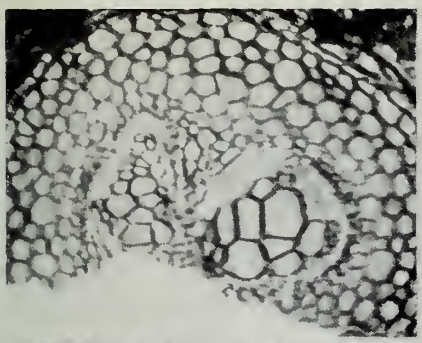
FIG. 4. T.S. of two small roots showing the piliferous layer, the exodermis and numerous root hairs, × 75. (Scott Coll., no. 1535).

Rhabdoxylon dichotomum nov. gen. et sp.

FIG. 5. T.S. of stem showing the emission of a monarch petiole trace. The loose texture of the inner cortex is well shown in the upper part of the section and its partial collapse on the sides and lower part. Note the firmer texture of the parenchymatous outer cortex, × 35. (Oliver Coll., no. K20k).

FIG. 6. T.S. of stem showing (*a*) equal forking of the stele and (*b*) the emission of a petiolar strand from the stem stele to the left of the figure, × 24. (Oliver Coll., no. K21r).

FIG. 7. T.S. of petiole showing the simple ovoid vascular bundle, the epidermis and traces of the surface hairs, × 25. (Kidston Coll., 2050).



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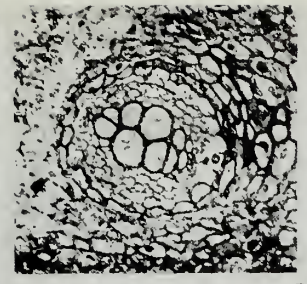

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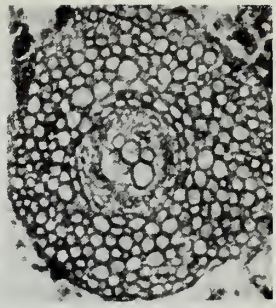

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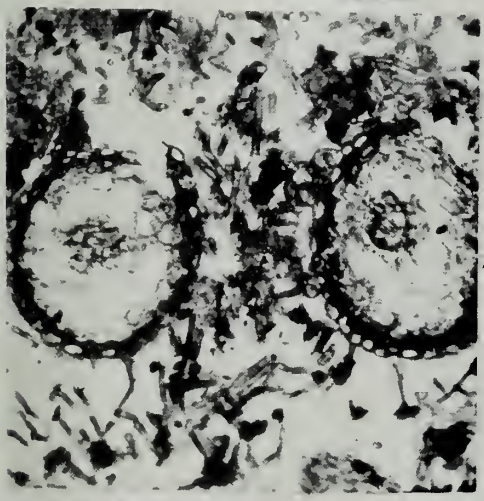

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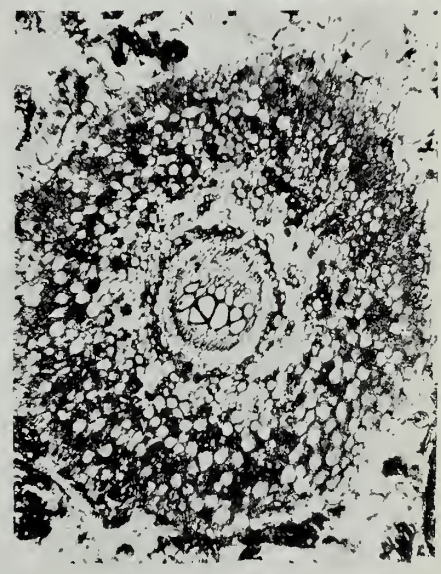

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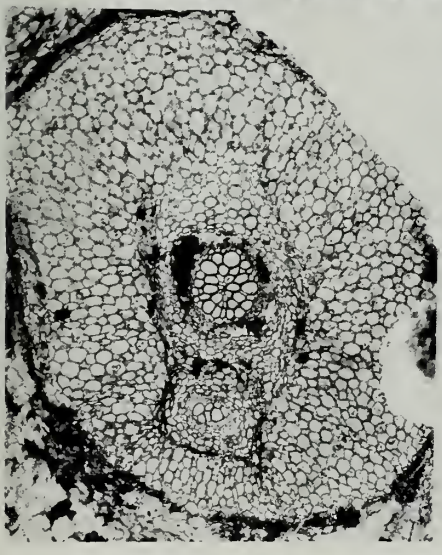

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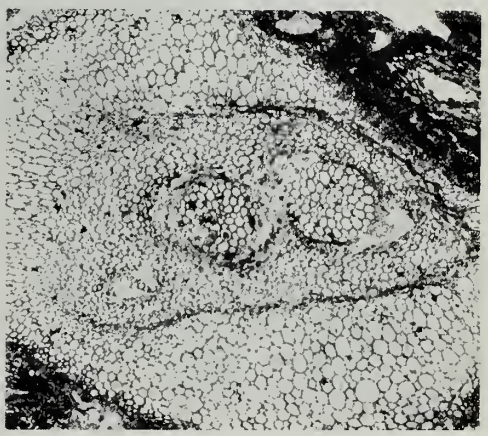

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